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# A risk assessment of Europe's black truffle sector under predicted climate change

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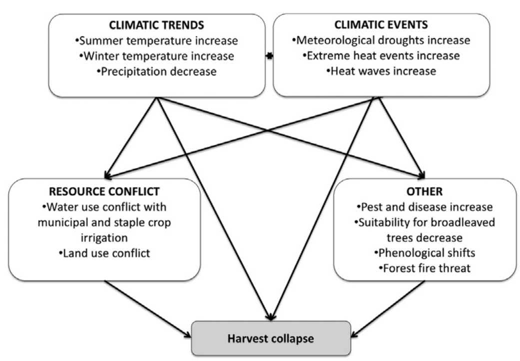
## HIGHLIGHTS

- Summer precipitation and summer temperature impact truffle production
- Declines of 78–100% in European truffle production are likely for 2071–2100
- Extreme weather events may accelerate the predicted truffle decline
- Truffles are surprisingly sensitive to summer temperatures

## GRAPHICAL ABSTRACT

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## ABSTRACT

The black truffle (*Tuber melanosporum*) is a highly revered culinary icon species that grows symbiotically with its host trees across several parts of southern Europe. Where harvested under natural or cultivated conditions, truffles can have a significant socioeconomic impact and may even form a key component of cultural identity. Although some aspects of truffle biology and ecology have been elucidated recently, the role of abiotic, environmental and climatic factors in the production and maturation of their fruitbodies is still largely unknown. Based on 36-year-long, continuous records of Mediterranean truffle yield, we demonstrate that decreased summer precipitation together with increased summer temperatures significantly reduce the fungus' subsequent winter harvest. Using state-of-the-art climate model projections, we predict that a significant decline of 78–100% in southern European truffle production is likely to occur between 2071 and 2100. The additional threats of forecasted heatwaves, forest fires, pest and disease outbreaks are discussed along with socioeconomic and ecological consequences of a warmer and dryer future climate. Our results emphasize the need for unravelling the direct and indirect effects of climate change on Europe's truffle sector and underline the importance of conservation initiatives at local to international scales.



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## 1. Introduction

Périgord black truffles are the highly valued hypogeal fruiting bodies of *Tuber melanosporum* (hereinafter, truffles). This culinary icon species regularly sells for prices well in excess of 1000 EUR/kg$^{-1}$ and reached 1300 EUR/kg$^{-1}$ at the end of the 2017–18 season (Martin et al., 2010, Laumont SL, personal communication, March 06, 2018). Yields may therefore provide a substantial contribution to some of southern Europe's rural economies (Büntgen et al., 2017), and further contribute to cultural identity through a range of societal activities (Samils et al., 2008). In those parts of north-eastern Spain, southern France, and northern and central Italy where truffles grow (Büntgen et al., 2012), either in their natural habitats or under widespread cultivation, numerous truffle museums exist and festivals have been dedicated to the fungus' rich winter harvest (Renowden, 2005).

In biological terms, truffles lack photosynthetic apparatus and the degradation ability of saprotrophic fungi, and therefore depend on plant-derived carbohydrates from a symbiotic partner *via* mycorrhizae (Smith and Read, 2010). Cultivation involves inoculating tree saplings with truffle spores and subsequent transplanting to suitable field sites (Chevalier and Sourzat, 2012), now accounting for an estimated ~80–90% of all commercially traded truffles in France (Reyna and Garcia-Barreda, 2014). The majority of Europe's truffle production is restricted to some regions in north-eastern Spain, southern France and northern-central Italy (hereinafter and collectively, the productive territory), where soil and climate conditions are favourable (Thomas, 2014; Hall et al., 2007). Due to negative effects of dry summers on the following winter truffle yield (Büntgen et al., 2012), irrigation has become a standard component of most of the plantations, not only in Spain but more recently also in France and Italy. The species distinct ecological requirements raise the question of how future climate change will impact the European truffle sector, directly and/or indirectly, at different spatiotemporal scales.

In order to better communicate results and to compare climate change studies, as well as in response to a request by the Intergovernmental Panel on Climate Change (IPCC; van der Linden and Hanson, 2007), a set of emission and socio-economic scenarios was developed that focus on possible development trajectories for the main forcing agents of future climate change. Termed Representative Concentration Pathways (RCPs), these state-of-the-art scenarios provide four trajectories for future atmospheric gas composition and land-use change up to the year 2100, compatible with the full range of emission scenarios available in the current scientific literature. A total of four RCPs were produced based on radiative forcing levels of 8.5, 6, 4.5 and 2.6 W/m$^2$ by 2100. RCP2.6 is a mitigation or 'peak and decline' scenario in which greenhouse gas emissions are substantially reduced. RCP4.5 and RCP6 are stabilization and reduction scenarios, and RCP8.5 is a scenario in which greenhouse gas emissions have a relatively high baseline. It should be noted that there are very few scenarios in the literature that correspond to RCP2.6 and many more that correspond to RCP8.5 (van Vuuren et al., 2011).

Here, we compare historical estimates of Spanish, French and Italian truffle production with climatic variations from the same regions to develop response functions of inter-annul to multi-decadal changes in southern European winter truffle yields and precipitation and temperature variations. A proxy-model assessment is then used to predict the likelihood of the effects of a warmer and drier future climate on the European truffle sector.

## 2. Methods

Although current trends point towards an increasing likelihood of RCP8.5, we also included RCP4.5 in our analysis in order to provide a greater range of impact under different climate change scenarios. In order to apply the RCP predictive models to truffle production, historical reports of truffle yields are correlated with climatic parameters, for each country of the truffle producing territory. Using these response curves and predictive climatic data for RCPs 4.5 and 8.5, we quantify the likely impact of different scenarios of future climate change on Europe's truffle harvest. Although areas within the truffle producing territory are characterized by broadly similar climatic conditions (Thomas, 2014), there are regional differences in the predicted climatic response to different emission scenarios (van Vuuren et al., 2011).

### 2.1. The historical dataset

A dataset covering the 36-year period from 1970 to 2006 for the three-main truffle producing countries in southern Europe was utilized (Büntgen et al., 2012). The dataset period was chosen so that it corresponded with the reference period for the utilized RCP predictive models. Information on annual truffle harvest from Spain (Reyna et al., 2005) and France (Courvoisier, 1995) was compiled by the national Truffle Grower Associations and published through the head organization Groupement European Tuber. Data from Italy were collected and published by the National Institute for Statistics (Pettenella et al., 2004). The data herein used, represents the most comprehensive chronological regional estimates of winter truffle production that are available. However, the precision of the data constrains the complexity of our statistical analysis as, for example, we are unable to account for differences in local practices such as irrigation (see discussion for a critical review of the available data and impact of local management practices). The winter truffle yield was plotted separately against June–August (JJA) averaged summer daily rainfall and temperature means. Monthly resolved temperature means and averaged summer daily rainfall were extracted from the gridded E-OBS database (Haylock et al., 2008). For north-eastern Spain, southern France and northern Italy, we restricted the climate data to equal domains: 40–42°N and 4°W to 2°E, 43–45°N and 0–6°E, as well as 44–46°N and 8–14°E, respectively. Winter temperatures are important as unusually cold conditions can damage maturing fruiting bodies (Chevalier and Pargney, 2014), but the RCP pathways unanimously point to warming and not cooling. Furthermore, summer temperature and precipitation are most important for truffle production (Molinier et al., 2013; Büntgen et al., 2012, 2015). Data were plotted in a linear form to observe absolute changes, individually for each region and the results were statistically analysed to produce $r^2$ values as well as confidence ranges (95%) and predictive intervals. Response curves were used to assess the likely impact of climate change on truffle production.

### 2.2. RCP scenario data

Data for predictive climate change under different RCP scenarios were created by the EURO-CODEX initiative (Jacob et al., 2014), which is part of an internationally coordinated framework to improve regional climate scenarios. This incorporates harmonisation of model evaluation and the generation of multi-model ensembles. The project involved 26 modelling groups contributing eleven different regional climate change models, herein considered the most robust and highest resolution (12.5 km) predictive dataset linked to different RCP scenarios.

## 3. Results

For all truffle producing territories, historical truffle production data correlated negatively with summer temperature means and positively with averaged summer daily rainfall (Fig. 1). The strongest relationships for temperature and precipitation were evident in Spain ($r^2 = 0.36$, $r^2 = 0.60$), followed by France ($r^2 = 0.33$, $r^2 = 0.29$) and Italy ($r^2 = 0.25$, $r^2 = 0.33$). Two significant outliers exist within the French dataset (Fig. 1) representing unusually high production in the years 1971 and 1972. In 1971, summer temperatures were moderate but rainfall levels were

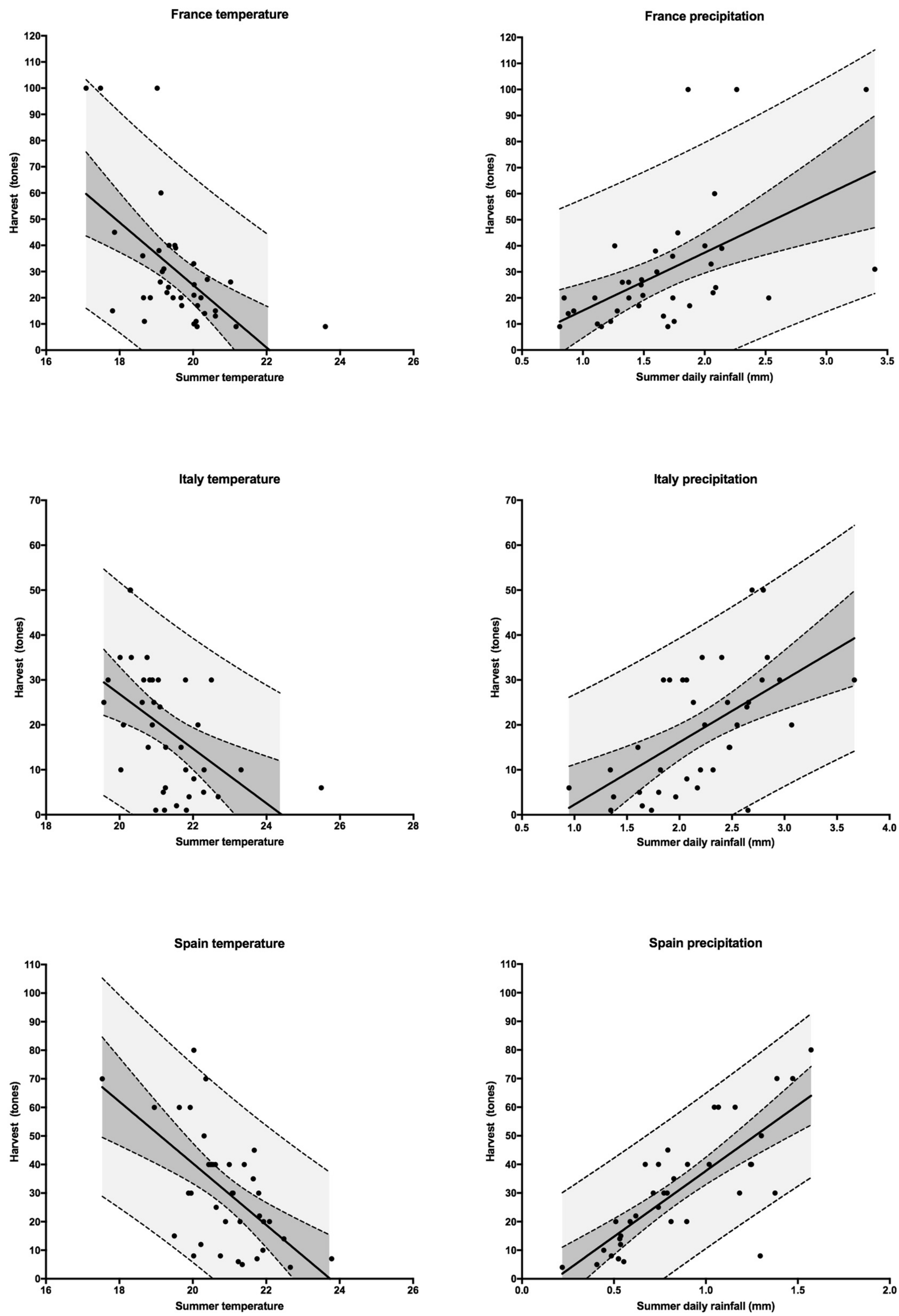


**Fig. 1.** Regression analysis for summer (JJA) temperature (left) and rainfall (right) for France, Italy and Spain plotted against annual truffle harvests for the period 1970–2006. Confidence level or range (95%) and predictive intervals are also displayed.

unusually high, *i.e.* the fourth wettest summer within the study period. For 1972, precipitation was moderate while it was the second coolest summer in the dataset. For Spain, there is also a high-production outlier in 1997, when temperatures were moderate but summer precipitation was the highest within the dataset.

### 3.1. Summer temperature under RCP 4.5 and 8.5

The RCP4.5 scenario for 2071–2100 predicts average summer temperature increases of 2–2.5 °C in France and 2.5–3.0 °C in Italy and Spain. This presents average summer temperature figures for the truffle

producing regions of 21.4–21.9 °C, 23.5–24.0 °C and 23.1–23.6 °C (Table 1), respectively. Using the response curves presented in Fig. 1, the likely negative impact on truffle yield of this temperature change, analysed in isolation of other climatic variables, is highly significant at 80.04%, 77.55% and 88.25% (Fig. 2), respectively. However, it should be noted that these predictions are based on figures from the tail-end of the dataset, with the impact on predictive confidence evidenced by the envelope of the 95% prediction intervals displayed in Fig. 1. The RCP8.5 scenario predicts a significantly larger summer temperature increase of 4–5 + °C for the French, 5 + °C for the Italian and 4.5–5.0 + °C for the Spanish truffle producing territories. This presents average summer temperature figures of 23.3–24.3 + °C, 26.0 + °C and 25.1–25.6 + °C (Table 1), respectively. Using the response curves presented in Fig. 1, the likely impact on yield is a total collapse of harvest, with the results predicting a value of 0 for all regions (Fig. 2). However, the degree of temperature impact under RCP8.5 means that predictions here must be based on extrapolations outside the range of existing data and this must be considered in interpretation of the results.

### 3.2. Summer rainfall under RCP 4.5 and 8.5

For total summer rainfall, the RCP4.5 scenario predicts a decline within the truffle producing regions of 15% for France, 10% for Italy and 15% Spain by 2071–2100. This presents average summer daily rainfall levels of 1.478, 2.057 and 0.750 mm (Table 1), respectively. Using the response curves presented in Fig. 1, the likely impact on yield of this decline in rainfall, analysed in isolation of other climatic variables, is a reduction of 14.01, 10.32 and 15.61% (Fig. 2), respectively.

The RCP8.5 scenario predicts a significantly larger summer rainfall decline of at least 25% for all three territories. This suggests maximum average summer daily rainfall levels of 1.304, 1.715 and 0.662 mm, respectively (Table 1). Using the response curves presented in Fig. 1, the likely impact on yield of this precipitation change, analysed in isolation of other climatic variables, is a minimum of 27.40, 36.18 and a 27.69% drop in annual harvests, respectively (Fig. 2). Predictive intervals for the data differ between each country with Spain showing the narrowest range (Fig. 1). This finding is in part attributed to Spain exhibiting the lowest overall summer precipitation of all three countries. The future yield levels will likely show significant inter-annual variation but are likely to locate within the predictive interval levels presented in Fig. 1. Further, it should be noted that although predictions for precipitation levels (in isolation) will have a significant impact on truffle yield, the greater threat is the predicted temperature increase.

## 4. Discussion

Since introduction of the RCPs (van Vuuren et al., 2011), global emissions have been tracked and these observations suggest consistent $CO_2$ levels just above the RCP8.5 pathway, leading to the assumption that this scenario is now likely for the 21st century (Sanford et al., 2014). Although we explore both the RCP4.5 and RCP8.5 scenarios, the increasing likelihood of RCP8.5 should be considered. Although we assessed summer temperature and precipitation statistically, other relevant climate change parameters, including heatwaves, droughts, forest fires, as well as pest and disease outbreaks, are also discussed.

### 4.1. Increased summer temperature

Truffles appear to have evolved from an epigeous ancestor (Bonito et al., 2013) and although the evolutionary pressures facilitating the transition from epigeous to hypogeous fruiting remains unclear, subterranean fruiting infers an advantage where local conditions may cause rapid desiccation of epigeous structures (Trappe and Claridge, 2005). Despite the protection afforded by hypogeal fruiting, it is not surprising that previous studies have shown that summer temperatures have an impact on quantity of truffle production (Molinier et al., 2013; Büntgen et al., 2015). Although our results agree that sporocarp production quantity is impacted by summer temperatures, the magnitude and significance of this impact is unexpected. The range of average temperature for the warmest month, of sporocarp-producing sites inside and outside of Europe is 15.8–25.0 °C (Thomas, 2014), and the data presented here suggest that the large variation in inter-site truffle yields seen in cultivation may in part be attributed to differences in summer temperatures. Unexpectedly, we also demonstrate that years with the lowest summer temperature records are associated with the highest production levels within the truffle producing regions with no lower limit identified (Fig. 1). This raises the intriguing prospect that the climatic optima for truffle production, may differ from the previously accepted necessity of a 'Mediterranean' climate (Chevalier and Sourzat, 2012). Recent evidence that truffles can be produced under much cooler conditions than previously realised, strengthens the hypothesis (Thomas and Büntgen, 2017). The newly reported sensitivity of truffles to summer temperatures accounts for the dramatic declines our predictive models display for production under RCP4.5 and total loss of production under RCP8.5 for the period 2071–2100 and beyond.

The declines presented in either scenario would have a strong impact on the truffle producing regions, not only in ecological but also economic terms. However, it is important to note that the predictive interval data displays a broad range, especially at the extremes of the dataset, and therefore a more likely scenario is that annual yields will display broad variability within this predictive range. Further and although the trend is clear, the predictions of yield under RCP8.5 are dependent on extrapolations outside the range of existing data and so care must be taken in their interpretation. Although the averaged production under RCP8.5 will likely be close to 0 there will be sites within each country that, due to local conditions, may still have some production. An example of this is varying moisture levels, which may have a significant impact on soil temperature (Hobbs, 1973; Wang et al., 2000). The relationship between soil moisture and temperature raises the prospect of using irrigation in an attempt to mitigate the predicted, local soil temperature increases.

**Table 1**
Summer (JJA) rainfall (Sum precip) and temperature means (Sum temp) for the reference period (1971–2000) and predicted changes under scenarios RCP4.5 and RCP8.5 for the period 2071–2100. Summer temperature gain displays predicted range of increase and predicted new average temperature range. Summer precipitation decline displays predicted range of decrease and new predicted precipitation level.

| | Sum temp (°C) | Sum temp gain (°C) and predicted av. temp RCP 4.5 | Sum temp gain (°C) and predicted av. temp RCP 8.5 | Sum precip (mm/day) | Sum precip decline (%) and predicted av. for RCP 4.5 (mm/day) | Sum precip decline (%) and predicted av. for RCP 8.5 (mm/day) |
|---|---|---|---|---|---|---|
| France | 19.31 | +2–2.5<br>21.31–21.81 | 4–5+<br>23.31–24.31+ | 1.74 | −5–25<br>1.48 | −25+<br>1.3 max |
| Italy | 20.99 | +2.5–3.0<br>23.49–23.99 | 5+<br>25.99+ | 2.29 | −15–+5<br>2.06 | −25+<br>1.72 max |
| Spain | 20.64 | +2.5–3.0<br>23.14–23.64 | 4.5–5+<br>25.14–25.64+ | 0.88 | −5–25<br>0.75 | -25+<br>0.66 max |

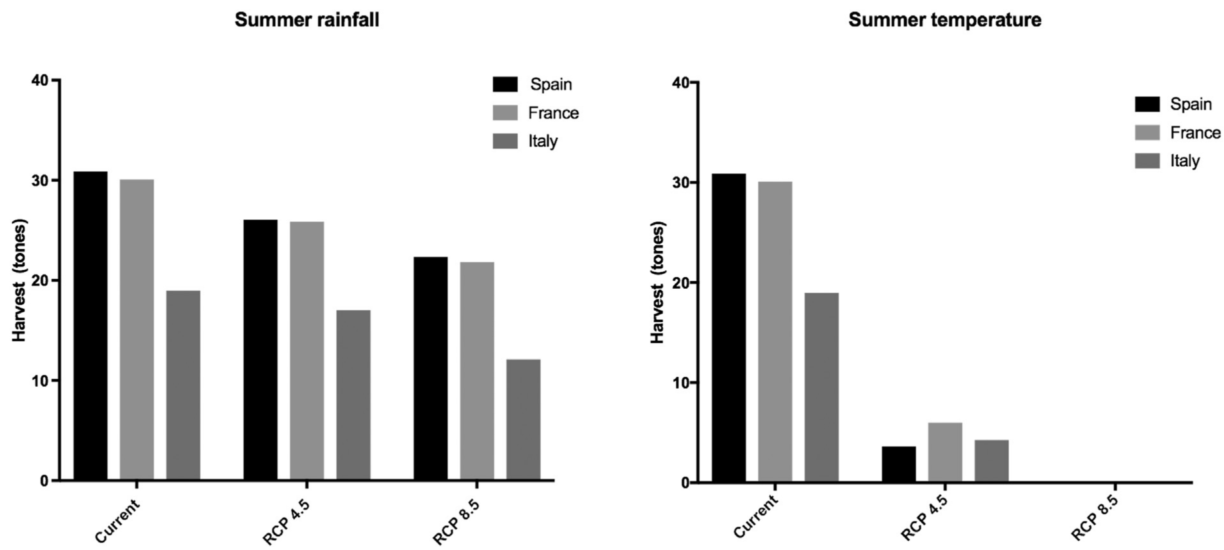


**Fig. 2.** Current average annual harvest (1970–2006) and predicted annual harvest for Spain, France and Italy under climate scenarios RCP4.5 and 8.5 (2071–2100) based on summer (JJA) rainfall and temperature predicted change. The predicted yield falls to 0 for the summer temperature scenario of RCP8.5.

### *4.2. Decreased summer precipitation*

Precipitation has previously been shown to be the most important climate factor for truffle production with drought events reducing truffle yields (Büntgen et al., 2012, 2015). Precipitation and the resultant impact on soil moisture levels are important not just as potential triggers for fruitbody initiation but also in fruitbody growth and maturation (Le Tacon et al., 2014) with 77.1% of the sporocarp being composed of water (Crisan and Sands, 1978). Under both RCP4.5 and 8.5 a significant decline in summer precipitation is expected and the predictive models also display a significant impact on truffle production. Although this agrees with the known sensitivity of truffles to precipitation, the degree of impact is significant but unexpectedly less than that of increasing temperatures. For example, the predicted impact of increasing temperatures under RCP4.5 is far higher than the impact of reduced precipitation under the more extreme RCP8.5. Whilst this may in part be attributed to the degree of impact on precipitation of the two pathways, it may also be an indication of the truffles' evolutionary development being partially driven by low moisture levels resulting in coping mechanisms (Trappe and Claridge, 2005). Spanish production showed the strongest correlation to summer rainfall and we suggest that this is because the region has the lowest average precipitation totals, meaning that a given percentage deviation from the mean has a more significant impact than in the other regions.

Although the predicted impact of trends towards reduced precipitation will have a significant impact on truffle yields, it is theoretically possible to mitigate this with adequate irrigation. However, this may not be achievable for two reasons: Irrigation use within existing orchards is already heavily restricted and regulated by the state in order to afford natural aquifers some protection and conserve resources for other uses, it would likely not be possible to increase this allocation and further, groundwater resources in many areas will continue to decline (see discussion below). For these reasons, any increase in irrigation to offset declining precipitation will likely not be possible. Further, more water will be needed, than that used to offset a decline in precipitation as increasing temperatures lead to increased evapotranspiration and reductions in base soil moisture levels (Füssel et al., 2017).

Finally, there remains the possibility that under different RCPs, the nature of rainfall may change to less frequent but higher volume events (Füssel et al., 2017). For this reason alone, the impact on truffle yields of decreased summer precipitation under the different RCP scenarios may be more or less significant that what is presented here.

### *4.3. Increased summer heatwaves*

Heatwaves are relevant when looking at the impact of climate change on biological systems as the potential impact can be very significant, compounding increases in averaged temperatures such as those we present above. In 2014, the Heat Wave Magnitude Index (HWMI) was introduced (Russo et al., 2014) as a means to give a standardised figure to the severity and duration of any heatwave event. The HWMI is defined as the maximum magnitude of heatwaves in a given year where a heatwave is ≥3 consecutive days with maximum temperatures above the 90th percentile of daily maxima for the reference period. The reference period for different RCP scenarios is set as 2006–2100, with data taken from 16 model simulations and each RCP analysed individually (Russo et al., 2014).

Very extreme heatwaves are defined as having a HWMI of above 8, the impact of this is highlighted when the figure is compared to the western European heatwave of 2003 which had an average HWMI of around 3. The 2003 western European heatwave created the hottest summer conditions since at least 1540, led to severe impacts on crops and was implicated in the deaths of an estimated 70,000 people across Europe (Robine et al., 2008). Multiple-model ensembles presented by Russo et al. (2014) predict that for 2068–2100 the truffle producing regions will experience very extreme heatwaves in 1–15 years in a 33-year period under RCP4.5 and in 12–33 years under RCP8.5. The truffle region of France will be marginally less impacted than the regions of Spain and Italy but even so, under RCP8.5 the best-case scenario for all regions would be experiencing an extreme heatwave biennially and a worst-case scenario would be such an event occurring annually. The impact of this on truffle production would be catastrophic and it should be noted that the truffle producing regions haven't experienced a HWMI ≥ 8 event since records began. Further, such events may occur in the very near future with Russo et al. (2014) also presenting analysis for the period 2020–2052 which incorporates an increased probability of such events.

A statistical analysis of the direct impact of the predicted increases in severity and duration of heatwaves on truffle production isolated by geographical region, is beyond the scope of this paper. The predictive increase in frequency, severity and duration of these events, will, however, have a very significant impact on truffle cultivation and will most likely lead to the collapse of truffle yields at numerous time points well before the predictive collapse of 2071–2100 (presented above) and further compounding the speed and intensity of this decline. As a point of reference, with a relatively low HWMI of 3 compared to the predicted

frequent future events with a HWMI of >8, the 2003 season was associated with an annual truffle yield across the regions of just 22.2% of the previous year harvest (22 *vs* 99 t). Finally, heatwaves and drought events often occur simultaneously and can strongly influence the impact of each other on biological systems.

### 4.4. Increased summer droughts

Drought event categories include, but are not limited to, meteorological, soil moisture and hydraulic droughts (Trnka et al., 2018). There are numerous statistical indices used to characterise meteorological droughts but all incorporate a measured reduction in precipitation in comparison to a 'normal' value, the impact of which is often compounded by an associated increase in temperature culminating in increased evapotranspiration. This may lead to both soil moisture droughts and eventually hydrological droughts, the latter of which is an impact on surface or sub-surface water supply and consequently the quantity and quality of water for irrigation (Van Loon, 2015). For the truffle producing regions, drought frequency and severity have already increased during the period 1950–2012 (Spinoni et al., 2015) whilst at the same time becoming less frequent and severe in other areas of Europe, notability northern and western Europe.

Extreme meteorological drought frequency, duration and area are predicted to increase substantially in the truffle producing regions under RCP4.5 and more substantially under RCP8.5. For example, Stagge et al. (2015) present an increase in extreme drought events of ~7-months in a 30-year period under RCP4.5 for 2041–2070 for much of the truffle producing regions, to an upper extreme of ≥15 months/30 years increase under RCP8.5 for the period 2071–2100 in Spain. Further, when evapotranspiration is incorporated, the predicted Mediterranean area to be affected by drought by the end of the 21st rises to 60% (Touma et al., 2015). The impact of precipitation on truffle production is most evident (Fig. 1). Although applying a statistical model to drought events, both in their predicted occurrence and the impact on truffle yield, is beyond the scope of this paper, it is clear that the predicted increases in drought events will compound the already sizeable declines. This creates a scenario in which we will see yields drop faster and with greater inter-annual variability than previously seen or predicted in Fig. 1. Moreover, increasing meteorological drought events will lead to increased hydraulic droughts (Van Loon, 2015; Trnka et al., 2018), which will increase water conflict from socioeconomic factors and reduce water availability for truffle-orchard irrigation. Further, the impact will be cumulative as trends towards reduced precipitation and increased drought events, lead to a gradual decline in surface and subsurface water reserves compounded by rising temperatures, heatwave events and other water use demands (Taylor et al., 2013; Füssel et al., 2017; Trnka et al., 2018).

### 4.5. Forest fires, pathogens and disease outbreaks

There are a number of other climate-induced variables that will likely have an impact on truffle harvest. Firstly, forest fires can have a significant direct impact on truffle cultivation by host plant destruction, as well as by impacting the soil chemistry, flora and fauna of a plantation. It is well known that fires can reduce ectomycorrhizal fungal communities although some species may benefit from the conditions created after the fire has passed (Glassman et al., 2015). Although the survival of truffle mycorrhiza after fire is unknown, it has been shown that new truffle cultivation is possible in post-fire situations, where the climate and natural soil type allow (De Aragón et al., 2012). Secondly, low tree-density truffle cultivation has been suggested as an activity within fire-break areas, maintaining a low combustible biomass level and an open structure in areas at risk from forest fires (Garcia-Barreda and Reyna, 2013).

However, although forest fires and fire-breaks may present an opportunity for expanding truffle cultivation, existing plantations are at risk from damage caused by these events. The risk of forest fires in the truffle producing regions is forecast to increase in terms of the area at risk as well as the length and severity of the fire season (Khabarov et al., 2016). The exacted impact of this increased risk is difficult to predict as implementation of protective measures such as fire breaks and behavioural changes may reduce the occurrence (Khabarov et al.,

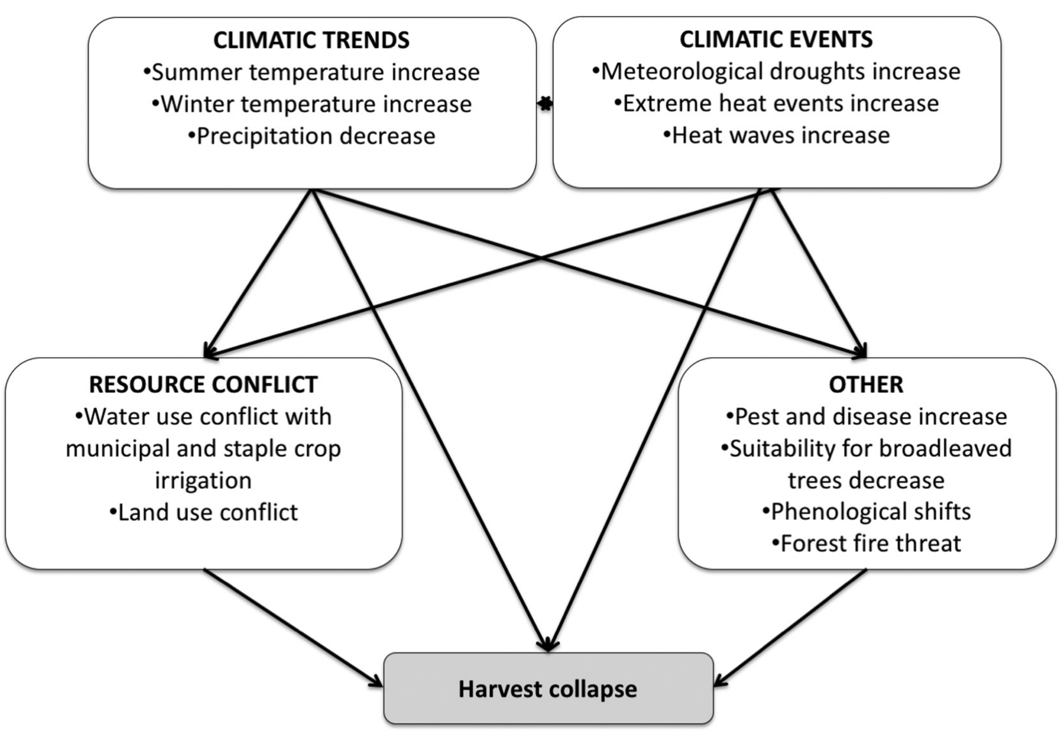


**Fig. 3.** Climate change routes to harvest collapse. Predicted future changes in climatic trends and events in scenarios RCP4.5 and RCP8.5 and compounded impacts resulting in harvest collapse.

2016). Although it is possible to increase the areas under truffle cultivation in response to forest fires and forest-fire protective measures, the risk of damage to established plantations will also increase under both RCP 4.5 and 8. It is not possible to predict the degree of impact on truffle yields, only to highlight the potential positives and negatives of such scenario.

Tree pests and disease incorporate a large range of organisms, all of which exhibit different climatic tolerances and needs. For example, *Phytophthora cinnamomi*, a destructive pathogen of oak trees, is forecast to significantly increase its range for the period 2070–2099, primarily driven by increasing winter temperatures within the study area (Bergot et al., 2004). Similar analysis has been done for a range of other pests and disease, some of which predict range shifts under predicted climate change (Barredo et al., 2015). There are many organisms that may impact the fruitbody (Rosa-Gruszecka et al., 2017) and the tree-partners in truffle cultivation and the potential response of many of these to climate change scenarios has not yet been elucidated. Thus, we do not yet know the direction of impact of a changing climate on pests and disease in general, but we do know that there will be a significant departure from the current landscape. This is an area that warrants more and deeper investigation, not just in reference to truffle cultivation but for other crops as well as conservation initiatives. Pest and disease are just one of a plethora of factors that may increase under climate change and can affect, jointly, truffle yields (Fig. 3), with a multitude of subsequent effects on regional ecology and economy.

## 5. Conclusions

Summer temperature and precipitation are dominant drivers of inter-annual to longer-term changes in winter truffle productivity, displaying high synchronicity and coherence between Spain, France and Italy. Although with statistical limitation, this study predicts, for the first time, a trend towards a likely collapse of some of the southern European truffle production under future warming by the end of this century (RCP8.5; 2071–2100). Consideration of other climate change related parameters further suggests that the failure could occur in advance of this date. The socio-economic impact of the predicted decline could be substantially larger as truffle harvesting and related activities form a key component of local history and cultural identity. These findings call for conservational initiatives to afford some protection to this important icon species. Action should include the expansion of truffle plantations into new territories of a more favourable future climate. Management strategies should further include mulching materials and cultivation practices to mitigate soil temperature fluctuations and conserve soil moisture.

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## References

Barredo, J.I., Strona, G., Rigo, D., Caudullo, G., Stancanelli, G., San-Miguel-Ayanz, J., 2015. Assessing the potential distribution of insect pests: case studies on large pine weevil (*Hylobius abietis* L) and horse-chestnut leaf miner (*Cameraria ohridella*) under present and future climate conditions in European forests. OEPP/EPPO Bull. 45 (2), 273–281.
Bergot, M., Cloppet, E., Perarnaud, V., Deque, M., Marcais, B., Desprez-Loustau, M.L., 2004. Simulation of potential range expansion of oak disease caused by *Phytophthora cinnamomi* under climate change. Glob. Chang. Biol. 10 (9), 1539–1552.
Bonito, G., Smith, M.E., Nowak, M., Healy, R.A., Guevara, G., Cázares, E., ... Murat, C., 2013. Historical biogeography and diversification of truffles in the *Tuberaceae* and their newly identified southern hemisphere sister lineage. PLoS One 8 (1), e52765.
Büntgen, U., Egli, S., Camarero, J.J., Fischer, E.M., Stobbe, U., Kauserud, H., ... Stenseth, N.C., 2012. Drought-induced decline in Mediterranean truffle harvest. Nat. Clim. Chang. 2 (12), 827–829.
Büntgen, U., Egli, S., Schneider, L., von Arx, G., Rigling, A., Camarero, J.J., ... Colinas, C., 2015. Long-term irrigation effects on Spanish holm oak growth and its black truffle symbiont. Agric. Ecosyst. Environ. 202, 148–159.
Büntgen, U., Latorre, J., Egli, S., Martínez-Peña, F., 2017. Socio-economic, scientific, and political benefits of mycotourism. Ecosphere 8 (7).
Chevalier, G., Pargney, J.C., 2014. Empirical or rational truffle cultivation? It is time to choose. For. Syst. 23 (2), 378–384.
Chevalier, G., Sourzat, P., 2012. Soils and techniques for cultivating *Tuber melanosporum* and *Tuber aestivum* in Europe. Edible Ectomycorrhizal Mushrooms. Springer, Berlin Heidelberg, pp. 163–189.
Courvoisier, M., 1995. La production et les cours de la truffe d'hiver 1903–1995. Le Trufficulteur Français. 10, pp. 8–9.
Crisan, E.V., Sands, A., 1978. Nutritional Value. Academic Press, New York, pp. 137–168.
De Aragón, J.M., Fischer, C., Bonet, J.A., Olivera, A., Oliach, D., Colinas, C., 2012. Economically profitable post fire restoration with black truffle (*Tuber melanosporum*) producing plantations. New For. 43 (5–6), 615–630.
van der Linden, P.J., Hanson, C.E., 2007. In: Parry, M., Canziani, O., Palutikof, J. (Eds.), Climate Change 2007: Impacts, Adaptation and Vulnerability. Vol. 4. Cambridge University Press, Cambridge.
Füssel, H.M., Jol, A., Marx, A., Hildén, M., Aparicio, A., Bastrup-Birk, A., ... Isoard, S., 2017. Climate Change, Impacts and Vulnerability in Europe 2016-An Indicator-based Report. EEA Report1977-8449 12.
Garcia-Barreda, S., Reyna, S., 2013. Cultivation of *Tuber melanosporum* in firebreaks: short-term persistence of the fungus and effect of seedling age and soil treatment. Fungal Biol. 117 (11), 783–790.
Glassman, S.I., Levine, C.R., Dirocco, A.M., Battles, J.J., Bruns, T.D., 2015. Ectomycorrhizal fungal spore bank recovery after a severe forest fire: some like it hot. ISME J. 10 (5), 1228.
Hall, I.R., Brown, G.T., Zambonelli, A., 2007. Taming the Truffle. Timber press.
Haylock, M.R., Hofstra, N., Klein Tank, A.M.G., Klok, E.J., Jones, P.D., New, M., 2008. A European daily high-resolution gridded data set of surface temperature and precipitation for 1950–2006. J. Geophys. Res.-Atmos. 113 (D20).
Hobbs, E.H., 1973. Crop cooling with sprinklers. Can. Agric. Eng. 15 (1), 6–8.
Jacob, D., Petersen, J., Eggert, B., Alias, A., Christensen, O.B., Bouwer, L.M., ... Georgopoulou, E., 2014. EURO-CORDEX: new high-resolution climate change projections for European impact research. Reg. Environ. Chang. 14 (2), 563–578.
Khabarov, N., Krasovskii, A., Obersteiner, M., Swart, R., Dosio, A., San-Miguel-Ayanz, J., ... Migliavacca, M., 2016. Forest fires and adaptation options in Europe. Reg. Environ. Chang. 16 (1), 21–30.
Le Tacon, F., Marçais, B., Courvoisier, M., Murat, C., Montpied, P., Becker, M., 2014. Climatic variations explain annual fluctuations in French Périgord black truffle wholesale markets but do not explain the decrease in black truffle production over the last 48 years. Mycorrhiza 24 (1), 115–125.
Martin, F., Kohler, A., Murat, C., Balestrini, R., Coutinho, P.M., Jaillon, O., ... Porcel, B., 2010. Périgord black truffle genome uncovers evolutionary origins and mechanisms of symbiosis. Nature 464 (7291), 1033–1038.
Molinier, V., Bouffaud, M.L., Castel, T., Mounier, A., Colombet, A., Recorbet, G., ... Wipf, D., 2013. Monitoring the fate of a 30-year-old truffle orchard in Burgundy: from *Tuber melanosporum* to *Tuber aestivum*. Agrofor. Syst. 87 (6), 1439–1449.
Pettenella, D., Klöhn, S., Brun, F., Carbone, F., Venzi, L., Cesaro, L., Ciccarese, L., 2004. Economic integration of urban consumers' demand and rural forestry production. Italy's Country Report. 30. COST Action E.
Renowden, G., 2005. The Truffle Book. Limestone Hills Ltd.
Reyna, S., Garcia-Barreda, S., 2014. Black truffle cultivation: a global reality. For. Syst. 23 (2), 317–328.
Reyna, S., De Miguel, A., Palazón, C., & Hernández, A. (2005). Spanish trufficulture. In: Proceedings of the Fourth International Workshop on Edible Mycorrhizal Mushrooms. Murcia, Spain, (28 November – 2 December). Universidad de Murcia.
Robine, J.M., Cheung, S.L.K., Le Roy, S., Van Oyen, H., Griffiths, C., Michel, J.P., Herrmann, F.R., 2008. Death toll exceeded 70,000 in Europe during the summer of 2003. C. R. Biol. 331 (2), 171–178.
Rosa-Gruszecka, A., Gange, A.C., Harvey, D.J., Jaworski, T., Hilszczański, J., Plewa, R., ... Hilszczańska, D., 2017. Insect-truffle interactions–potential threats to emerging industries? Fungal Ecol. 25, 59–63.
Russo, S., Dosio, A., Graversen, R.G., Sillmann, J., Carrao, H., Dunbar, M.B., ... Vogt, J.V., 2014. Magnitude of extreme heat waves in present climate and their projection in a warming world. J. Geophys. Res.-Atmos. 119 (22).
Samils, N., Olivera, A., Danell, E., Alexander, S.J., Fischer, C., Colinas, C., 2008. The socioeconomic impact of truffle cultivation in rural Spain. Econ. Bot. 62 (3), 331.
Sanford, T., Frumhoff, P.C., Luers, A., Gulledge, J., 2014. The climate policy narrative for a dangerously warming world. Nat. Clim. Chang. 4 (3), 164–166.
Smith, S.E., Read, D.J., 2010. Mycorrhizal symbiosis. Academic press.
Spinoni, J., Naumann, G., Vogt, J., Barbosa, P., 2015. European drought climatologies and trends based on a multi-indicator approach. Glob. Planet. Chang. 127, 50–57.
Stagge, J.H., Kohn, I., Tallaksen, L.M., Stahl, K., 2015. Modeling drought impact occurrence based on meteorological drought indices in Europe. J. Hydrol. 530, 37–50.
Taylor, R.G., Scanlon, B., Döll, P., Rodell, M., Van Beek, R., Wada, Y., ... Konikow, L., 2013. Ground water and climate change. Nat. Clim. Chang. 3 (4), 322–329.
Thomas, P., 2014. An analysis of the climatic parameters needed for *Tuber melanosporum* cultivation incorporating data from six continents. Mycosphere 5 (1), 137–142.
Thomas, P., Büntgen, U., 2017. First harvest of Périgord black truffle in the UK as a result of climate change. Clim. Res. 74 (1), 67–70.

Touma, D., Ashfaq, M., Nayak, M.A., Kao, S.C., Diffenbaugh, N.S., 2015. A multi-model and multi-index evaluation of drought characteristics in the 21st century. J. Hydrol. 526, 196–207.
Trappe, J.M., Claridge, A.W., 2005. Hypogeous fungi: evolution of reproductive and dispersal strategies through interactions with animals and mycorrhizal plants. Mycol. Ser. 23, 613.
Trnka, M., Hayes, M., Jurečka, F., Bartošová, L., Anderson, M., ... Büntgen, U., 2018. Priority questions in multidisciplinary drought research. Clim. Res. https://doi.org/10.3354/cr01509.
Van Loon, A.F., 2015. Hydrological drought explained. Wiley Interdiscip. Rev. Water 2 (4), 359–392.
Van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., ... Masui, T., 2011. The representative concentration pathways: an overview. Clim. Chang. 109 (1–2), 5.
Wang, D., Shannon, M.C., Grieve, C.M., Yates, S.R., 2000. Soil water and temperature regimes in drip and sprinkler irrigation, and implications to soybean emergence. Agric. Water Manag. 43 (1), 15–28.